

THE CASE FOR THE THYLACOMYIDAE AND MYRMECOBIIDAE, GILL, 1872, OR WHY ARE MARSUPIAL FAMILIES SO EXTENDED?

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Synopsis

Recognition by almost all modern workers of *Myrmecobius* and *Macrotis* as taxa distinct only at the sub-family level is a result of the somewhat compressed marsupial classification of previous years. Given the expanded hierarchy now in use (e.g. that of Kirsch, 1968), marsupial classification will have greater uniformity at the family level if these two taxa are raised in rank.

Historically, *Myrmecobius* (the numbat) has always been recognised as very distinct, largely because of its supernumerary molars. All of its cheek-teeth differ from the tribosphenic pattern of other dasyuroids. Its basicranium also differs from other dasyuroids and indicates an early divergence of *Myrmecobius*. Serologically it is less distinct; that it is not more so may be due to a low rate of change in serum antigens. Its chromosomes are very similar to those of other dasyuroids, but non-dasyuroid families display the same karyotype.

Rabbit-eared bandicoots were first recognised as a subfamily by Bensley (1903), because the squaring of their molars involves the metacone rather than the hypocone (modified metaconule) of other perameloids. The basicranium also departs from the presumably ancestral morphology, although it is convergently similar to that of *Isoodon*. *Macrotis* is serologically distinct from other perameloids, and the chromosomes are so different that they could not have been derived directly from the peramelid pattern. *Ischnodon* is a fossil form manifestly allied with *Macrotis*.

Myrmecobiidae has previously been used (e.g. by Gregory, 1910) in the same sense as it is here; Thylacomyiidae derives from Bensley's (1903) usage and must be retained, though it is based on a generic name since shown to be invalid.

INTRODUCTION

Contemporary classifications represent an attempt to reconcile the sometimes contradictory demands of phylogenetic and practical groupings. Broad relationships of organisms are expressed in a rather free way; but at lower categorical levels an effort is made to have genera and families represent comparable degrees of divergence, so that the same amounts and kinds of information about the organisms are encoded or implied in the classification. This approach to uniformity is necessary if a classification is to be of heuristic value to non-taxonomic biologists, and if generalisations from the characteristics of one to those of many species are to be possible. If the groupings contain too broad a range of forms, or uneven degrees of difference within co-ordinate groups, such predictions can only be made with low confidence.

Marsupial classification has undergone considerable re-assessment in recent years, particularly in terms of the major classification (e.g., Ride, 1964; Kirsch, 1968), as well as in revision and grouping of certain genera. On the intermediate levels, eleven families of living Australian marsupials are now recognised (Ride, 1970), compared with Simpson's six (1945). The reasons for this increase do not include discovery of unknown forms, but rather reconsideration of the status of the known animals. Thus, one of the "new" families, Thylacinidae, is recognised because of the thylacine's great distinctness from the other dasyuroids; the erection of another, Phascolarctidae, is consequent on appreciation of the considerable evidence that the koala is not a phalangerid but has wombats as its nearest relatives. Three additions to the list are

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Burramyidae, Petauridae, and Tarsipedidae, formerly included in Phalangeridae, which Kirsch (1968) recognises on serological and other grounds.

Each of these new families is thus soundly based, and their recognition reflects attempts to indicate both correct affinities and equivalent levels of distinctness and diversity at this categorical level. In our desire to bring marsupial classification even closer to an ideal uniformity, we propose here the recognition of two more marsupial families, Myrmecobiidae and Thylacomyidae, represented by the genera *Myrmecobius* and *Macrotis* (with *Isechnodon*) respectively. We review aspects of the history of their classification, adduce some recently-published evidence bearing on each case, and present new morphological evidence for regarding them as distinct at the family level.

MYRMECOBIIDAE, Gill, 1872

Historical

From the time of its description, the numbat was recognised as something very special. Its high dental formula and appearance of the teeth led Owen (1840-45) to describe *Myrmecobius* as a near relative of certain Mesozoic mammals which were then thought to be marsupials. This opinion was common throughout most of the 19th century, and although Thomas (1888) places *Myrmecobius* in a subfamily of the Dasyuridae, he considers that it might well be separated at a higher level. Bensley (1903), after carefully examining the dentition, concludes that it could be derived from the dasyurid condition, an opinion which is accepted by us, but which has encouraged the view that the numbat and dasyurids have a rather close affinity. Tate (1951) seems not to have committed himself on the precise level of the numbat's distinctness, and Ride (1970) regards it as a dasyurid in his more recent classification. Nevertheless, a number of twentieth-century taxonomists (Gregory, 1910; Cabrera, 1919; Jones, 1923-25; Troughton, 1967) place *Myrmecobius* in its own family.

In view of what we now know about the evolution of Mesozoic mammals, and of marsupials, it is impossible that the numbat should be "... an unmodified survivor from Mesozoic times . . ." (Thomas, 1888, p. 312), but, on the other hand, we might ask if the placement of it in a subfamily of dasyurids is not an extreme alternative, and partly a result of the somewhat compressed marsupial classification of previous years: it will be remembered that Bensley also placed *Thylacinus* in a subfamily of Dasyuridae, while regarding it as a foreign element in the Australian fauna.

Cranial and Dental Morphology

Myrmecobius, although clearly a dasyuroid, differs from all dasyurids in many basicranial and dental characteristics. The unity of the Dasyuridae has been established with regard to serology (Kirsch, 1968), cytology (e.g., Sharman, 1961; Hayman and Martin, 1974), the dentition (Archer, 1976a) and the basicranium (Archer, 1976b).

Myrmecobius is excluded from the Dasyuridae for the following dental reasons. First, it has variably developed supernumerary molariform teeth (4/5 to 5/6). Bensley's (1903) description of a juvenile specimen with a minute anterior molariform tooth casts doubt on Winge's (1941) hypothesis that the deciduous tooth is retained in the adult dentition and accounts for one of the supernumerary molariform teeth in each tooth row. The normal presence of more than four molariform teeth in *Myrmecobius* is unique among marsupials although supernumerary molars are found in some macropodid and dasyurid individuals (Archer, 1975). The crown morphology of the upper molars is only marginally reminiscent of a tritubercular pattern and is certainly not trituberculo-sectorial. The lower molariform teeth are similarly specialised. In the upper teeth the buccal cusps are dominant (possibly homologues of

dasyurid styler cusps) and in the lower teeth the lingual cusps are dominant (probably homologues of the paraconid, metaconid, entoconid and hypoconulid). The only clear dental similarity to dasyurids is the incisor number and in any case this is not unique to dasyurids. It is present in thylacinids, some borhyaenids and some peramelids.

The basicranium of *Myrmecobius* is most similar to that of dasyurids. Significant points in common include the lack of a foramen ovale (a foramen pseudovale is present), and the presence of an imperforate stapes and a well-developed squamosal epitympanic sinus. None of these characteristics is individually confined to dasyurids and *Myrmecobius*, but as a combination of characteristics, it is unique. *Myrmecobius* significantly differs from dasyurids in virtually lacking a periotic hypotympanic sinus; in having the alisphenoid tympanic wing contacting the mastoid tympanic wing (a condition otherwise confined to certain phalangeroids); in having an antero-mesially extended alisphenoid hypotympanic sinus; in having a poorly enclosed internal jugular canal (a condition found in didelphids and peramelids); and in the posterior development of the pterygoids which underlie the transverse canal as well as forming part of the rim of the entocarotid foramen.

Other important differences that distinguish *Myrmecobius* include the posteriorly extended palate; the postero-ventral crest of the jugal; the massive post-orbital frontal processes; the lacrymal which extends well out onto the face; the large interparietal; the complete postero-lateral palatal foramen; the ventral position of the infraorbital foramen on the maxilla; and the reduced squamosal contribution to the zygomatic arch. These are all non-dasyurid features, and in many cases are unique among marsupials.

The basicranial region indicates that the ancestor of the myrmecobiids was probably a dasyurid rather than a didelphid. However, that ancestor lacked many features present in all other dasyurids (such as a periotic hypotympanic sinus) and was obviously undergoing unique specialisations not present in any known dasyurid lineage.

Fossil myrmecobiids are unknown, and we can only speculate about the history of the group. The lack of a periotic hypotympanic sinus suggests the divergence from a dasyurid lineage was an early one, probably before the late Miocene by which time many modern dasyurid lineages had become established.

Serology

Myrmecobius is clearly distinct serologically from other dasyuroid genera. This is indicated in Kirsch (1968), where the amount of divergence is suggested to be about the same as that separating subfamilies in other marsupial families.

However, this does not dictate that the numbat should be considered only as representative of a subfamily. It is also true that the koala and wombats are serologically distinct at a subfamilial level, but Kirsch argues that morphological differences clearly warrant familial recognition in that case. *Phascolaretids* are moreover an old and structurally ancestral family (Archer, 1976c) with many *Phascolaretos*-like forms occurring in middle Tertiary deposits which are among the oldest known mammal-bearing sediments in Australia. Vombatids also occur in these deposits. This suggests that the serum antigen evolution of one or both of these groups has been relatively conservative in comparison with their cranial and dental evolution.

It may similarly be argued that *Myrmecobius* is serologically conservative, accounting for its rather great similarity to the dasyurids, and this contention is supported by evidence for special serological similarities between it and *Phascolaretos* which seem too numerous to be convergent (Kirsch, in preparation). The numbat-koala affinity does not imply a special phylogenetic relationship

between the two genera, but does strongly suggest that each lineage has evolved more slowly than its nearest relatives, and has retained a greater proportion of ancestral antigens.

Karyology

The numbat has $2N=14$ chromosomes, a number also exhibited by caenolestids, dasyurids, peramelids (in the restricted sense used here by us), some didelphids and many phalangeroids. In most of these cases chromosome morphology is also similar (Hayman and Martin, 1974). Therefore chromosome number neither allies *Myrmecobius* solely with, nor differentiates it from, dasyurids.

Family Name

The derivation of the family name Myrmecobiidae is obvious. It has been used in the sense in which we use it by Gill (1872), Iredale and Troughton (1934), and by authors cited above.

THYLACOMYIDAE

Historical

Unlike *Myrmecobius*, *Macrotis* was not regarded as being particularly distinctive until 1903 when Bensley pointed out its strikingly unusual molar morphology. Prior to this time it was not separated taxonomically from other perameloids at anything other than a generic level.

The antiquity of the rabbit-eared bandicoot lineage has been demonstrated by Stirton (1955) with the description of *Ischnodon australis*, a Tertiary (possibly lower Pliocene) bandicoot related to *Macrotis*.

Cranial and Dental Morphology

It has been suggested as a result of a broader study of the basicranial region of carnivorous and insectivorous marsupials (Archer, 1976b) that perameloids originated from didelphoids. Both groups include structurally ancestral forms with a very small alisphenoid tympanic wing, virtually absent periotic tympanic wings, a simple shallow epitympanic recess, and a poorly-developed or absent squamosal epitympanic sinus. The peramelid genera *Peroryctes*, *Microperoryctes*, *Perameles* (most species) and to a lesser extent *Echymipera* show this fundamentally simple basicranial pattern. The perameloid genera *Macrotis*, *Isoodon* and to a lesser extent *Chaeropus* show marked departures from this structurally simple condition. In *Perameles nasuta* a shallow basin occurs in the lateral extension of the periotic. This basin is the clear homologue of the epitympanic recess. In *Isoodon*, the roof of the epitympanic recess is partly reformed in a way analogous to the development of the false palate in mammals. The homologue of the roof of the epitympanic recess in didelphids is displaced dorsally and an analogue is formed by converging horizontal plates of the squamosal and periotic bones. The incudal fossa remains unaffected. As noted elsewhere (Archer, 1976b), the invaginated portion of the epitympanic recess in *Isoodon* is the dorsal periotic epitympanic sinus. *Chaeropus* is structurally intermediate between the conditions found in *Perameles* and *Isoodon*. In *Macrotis*, besides enlarged periotic and alisphenoid hypotympanic sinuses such as occur in *Isoodon*, there is also an enlarged dorsal periotic epitympanic sinus. It differs from that of *Isoodon* in being smaller and in having a relatively much lower sphenoid septum to act as an anterior wall. The condition found in *Macrotis* could be derived from that in *Peroryctes* or some *Perameles*, and be convergent on the condition seen in *Isoodon*. The position of the foramen ovale relative to the alisphenoid hypotympanic sinus also differs in *Macrotis* and *Isoodon*. In *Isoodon* the anterior

end of this sinus passes within the alisphenoid mesial to the foramen ovale. In *Macrotis* it passes lateral to the foramen ovale. A structurally ancestral condition common to both may be found in some peramelines such as *Peroryctes* where the foramen ovale occurs at the anterior end of the alisphenoid hypotympanic sinus rather than to one side.

Basiscranial structure therefore separates structurally ancestral perameloids such as *Perameles* and *Peroryctes* from specialised forms such as *Isoodon*, *Chaeropus* and *Macrotis*. Overt similarities in size of the hypotympanic and epitympanic sinuses between *Isoodon* and *Macrotis* evidently result from convergence and a common ancestral condition must have structurally resembled that seen in modern *Peroryctes* or *Perameles*.

Bensley (1903) demonstrates the polyphyletic origin of quadrate molars in perameloids. In peramelids, the hypocone is a modified metaconule, a fact clearly seen in the structural lineage from *Peroryctes*, through *Perameles*, to *Isoodon*. Only in *Macrotis* (and presumably *Ischnodon*) is the postero-lingual cusp position occupied by the metacone. The metacone of *Macrotis* is not, however, analogous in function to the topographic hypocone of even the quadritubercular peramelid *Isoodon*. The relatively very low hypocone of peramelids indicates a different use for this cusp than is served by the very high metacone of *Macrotis*. The serial homologues of the metacone, styler cusp B and metaarista of *Macrotis* are those same cusps in peramelids. *Macrotis* is unique among perameloids in lacking a metaconule (the hypocone of peramelids such as *Isoodon*). It is further unique in possessing a large and discrete styler cusp B immediately buccal to the paracone of M^1 . In all other perameloids in which this molar region is known, styler cusp B on M^1 is either indistinguishable or small, and well-united or postero-buccal to the paracone. *Macrotis* has a much enlarged and longitudinally elongate styler cusp D on M^{1-3} , a condition which is also unique among perameloids. Stirton (1955) suggests that *Ischnodon* may have been ancestral to *Macrotis*. Nothing about the dental morphology prohibits this possibility. Lower molars of *Macrotis* and *Ischnodon* differ in that in *Ischnodon* the anterior cingulum is relatively less developed, particularly so in M_1 , the paraconid is well developed and the molars are relatively much lower-crowned. Stirton (1955) notes the larger paraconid and low-crowned condition. Ride (1964) disputes the diagnostic value of the paraconid size and suggests that some specimens of *Macrotis* show a similar condition. Having examined a large collection of juvenile *Macrotis* (including Queensland Museum JM769), it is clear that Stirton (1955) is at least partly correct in regarding *Macrotis* to have the paraconid reduced or absent. M_{2-3} invariably have the paracristid either merging onto the antero-buccal flank of the metaconid, or terminating just short of that cusp. The antero-lingual corner of these molars is formed by the lingual end of the very well developed anterior cingulum. On M_1 , however, the paraconid is invariably present (on specimens examined at the Queensland Museum). There is no paracristid and the anterior cingulum is reduced to a small antero-lingual cusp which occurs below the paraconid. The only known specimen of *Ischnodon* has a similar M_1 cusp morphology (and in this regard Ride, 1964, is correct in observing little difference between the genera) but the M_2 is markedly different from *Macrotis*. The paracristid is well developed and extends past the metaconid to the lingual edge of the crown, forming a clear paraconid. The antero-lingual edge of the less well developed anterior cingulum is reduced. Further, the buccal end of this cingulum is separated from the base of the protoconid by a fissure. In *Macrotis* the buccal end swings high up on the protoconid, merging with that cusp only a short distance down from the apex of the cusp.

With the addition of the less specialised *Ischnodon* to the Thylacomyidae, this group of bandicoots exhibits a lower molar morphology which is more

similar to that of peramelids than is the morphology of the upper molars. Upper molar morphology suggests that thylacomyids evolved from peramelids before peramelids modified the metaconule into a hypocone and altered the position and size of the styler cusps. A structurally ancestral condition of this sort is most closely approximated among living peramelids by *Peroryctes* and *Microperoryctes*, but even here the metaconule is pronounced and the styler cusps are clearly unlike those of thylacomyids.

It is evident that the perameloid radiation resulted in two fundamentally different groups, the thylacomyids (including *Macrotis* and *Ischnodon*) and the peramelids (including all other genera). The morphology of the auditory region and teeth indicate that the two groups could have had a common ancestor structurally most similar among modern peramelids to *Peroryctes* of *Microperoryctes*, but even more generalised than these structurally primitive peramelids.

Despite the removal by us of rabbit-eared bandicoots from the Peramelidae, it is still apparent that further taxonomic groupings within the Peramelidae may eventually be advisable. In particular, *Chacropus* and *Isodon* are morphologically very distinct (but less so than *Macrotis*) from all other perameloid genera as well as from each other.

Serology

Macrotis is serologically distinct from all other perameloids. As is the case with *Myrmecobius*, this is indicated by Kirsch (1968) to be about equivalent to subfamilial divergence in other marsupial groups.

No dramatic special serological affinities, such as obtained between the numbat and koala, can be demonstrated for *Macrotis*. Rather, its peculiarity is that, of the several perameloids tested, it alone did not group closer to the dasyurids than to the Australian diprotodont marsupials. *Macrotis* is thus peculiar in respect of perameloid affinities as well as in being distinct within the group.

Karyology

The chromosomes of *Macrotis* ($2N=18 \text{ ♀}$, 19 ♂ (Martin and Hayman, 1967)) are very different from those of other bandicoots, and are probably derived from a higher number than 14 (the number in all dasyurids and known peramelids as well as in some other families or members of them). Martin and Hayman (1967) state, in fact, that the *Macrotis* karyotype, with its higher number and XX/XY₂ sex-determining mechanism, cannot be derived directly from the peramelid pattern; rather, the reverse. They are now (Hayman and Martin, 1974) inclined to derive *Macrotis* from an intermediate higher-numbered form itself derived from a perameloid. Sharman (1973) suggests that the peramelid karyotype could be a reduction from a higher number and not merely a modification of the dasyurid karyotype, as Hayman and Martin (1974) contend. Whether peramelid and thylacomyid karyotypes each derived from a common ancestral higher number, or whether the peramelid pattern is primitive, with the pattern of *Macrotis* being a secondary reduction from some intermediately higher number, it is certain that the karyotypes of peramelids and of *Macrotis* are separated by several steps unrepresented among extant bandicoots. No marsupial family except Macropodidae shows as great a range of numbers and sex-determining mechanisms.

Thylacomys and the Family Name *Thylacomyidae*

In 1838 an anonymous article appeared in the London *Athenaeum* (No. 572, 13th October, p. 747) stating "The reading of an elaborate paper, descriptive of the osteology of the *Marsupialia*, was commenced by Mr. Owen, who remarked upon the great value of an acquaintance with the structure of the skeleton

in determining the genera and species of this group of animals, and proposed a new genus, *Thylacomys*, for certain species presenting a peculiar confirmation of the cranium". There can be no doubt that this does not constitute a description and the name is a *nomen nudum*, a conclusion also reached by Thomas (*in* Waite, 1900), Sherborn (1931), Troughton (1932), and Neave (1940). Owen (1838) in discussing the rabbit-eared bandicoots refers only to *Perameles lagotis* appearing carefully to avoid using the term *Thylacomys* which he evidently had used during the reading of his paper. For this reason we agree with Palmer (1899) who suggests Owen should not be held as the author of *Thylacomys*. Blyth, in Cuvier's *Animal Kingdom* (1840), p. 104, does provide a generic description of the rabbit-eared bandicoots, but under the name *Thulacomys*. We regard this spelling to be an error for *Thylacomys* (Article 33b, Rules of Zoological Nomenclature) as do Thomas (*in* Waite, 1900), Sherborn (1931), Troughton (1932), and Neave (1940). In agreement with Palmer (1899), we therefore regard *Thylacomys* to have been described by Blyth in 1840.

The derivation of the familial name for the rabbit-eared bandicoots, now all regarded (e.g. by Troughton, 1932) as *Macrotis*, is not immediately obvious. Until recently, *Thylacomys* was generally regarded as the valid generic name for these bandicoots, and Bensley (1903) consequently uses it as the basis of his subfamily name, Thylacomyninae. By the rules of the Code (Article 40), a family-group name need not be changed even though the name of the type genus is subsequently shown to be invalid and is replaced, if the original family-group name has won general acceptance. This is the case here and the family name should therefore be Thylacomyidae.

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